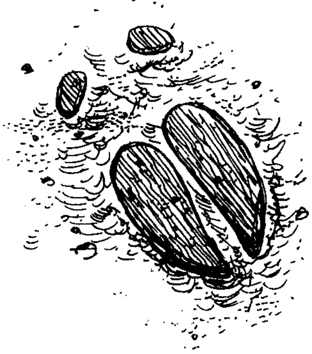
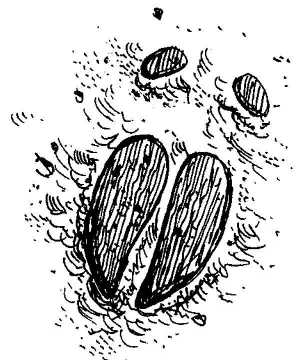
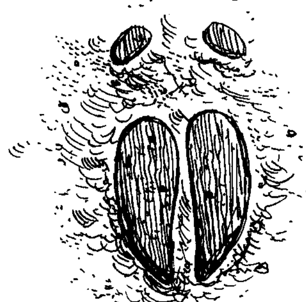
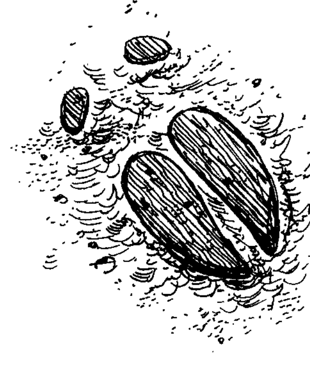


Part II

Modeling








D.C.

Executive Summary of Model-Based Assessment of Elk in the Rocky Mountain National Park Ecosystem

By

Michael B. Coughenour

Natural Resources Ecology Laboratory
Colorado State University
Fort Collins, Colorado 80523

Rocky Mountain National Park (RMNP) was established after a period of substantial resource extraction by early settlers, including trappers, hunters, miners, loggers, and ranchers. A once abundant large herbivore, elk (*Cervus elaphus*) had by that time been extirpated from the region by a period of intensive market hunting in the 1860s and 1870s (Guse 1966). Mule deer (*Odocoileus hemionus*) were also much reduced. Elk were reintroduced in 1913–1914, and the population grew in size to approximately 900 animals in 1938–1939 (Packard 1947a). Elk were intensively managed from 1944–1968, due to early concerns that they were overabundant, and damaging the winter range. The herd was reduced by culling operations in 1944–1945 and 1949–1950, and generally kept in the 300–600 range through 1968. Public disapproval of elk culling in Yellowstone led to an experimental approach to management often referred to as natural regulation. The hypothesis was that elk would reach a natural food-limited carrying capacity, and population growth would be self-regulated through density-dependent competition for food. Since 1968, the elk herd in RMNP has been managed only by sport hunting outside of the park boundary, which has not controlled elk population growth. Furthermore, elk have been increasingly wintering outside the park boundaries in the town of Estes Park, where they also largely escape hunting.

Concerns about elk impacts on plants and other components of the ecosystem have heightened considerably during the last two decades (Olmsted 1977, 1979, 1997; Hess 1993; Wagner et al. 1995; Baker et al. 1997; Berry et al. 1997; Keigley and Wagner 1998). In particular, it has been suggested that elk are overabundant and present in unnatural densities due to lack of natural predators and Native American hunting. These authors felt that in pre-settlement times, elk were present at much lower densities, and they may not have wintered in the areas that now comprise RMNP. However, there appears to be no evidence that elk did not winter on the eastern slope of the park in historic times.

An effort was made to review the literature for prehistoric and historic elk presence. Prehistoric game drive systems discovered at high elevations within the park were most likely used to hunt elk (Benedict 1992, 1999). There was a considerable amount of historical evidence of elk presence prior to settlement (Sage 1846; Loring 1893; Sprague 1925; Fryxell 1928; Estes 1939).

Human impacts on the elk winter range prior to the creation of the national park provided an unnatural starting point for the elk reintroduction program, and likely exacerbated elk impacts on the range. Livestock grazing was widespread and apparently intense enough to cause significant changes in herbaceous vegetation cover (Mills 1924; McLaughlin 1931; Ratcliff 1941). Land had also been drained and willows cut to support haying operations (Gysel 1960).

A deer eruption in the 1930s, along with increased numbers of elk, brought about declines in upland shrubs (Ratcliff 1941), willow cover (Dixon 1939; Gysel 1960), and barking and suppression of regeneration in aspen (McLaughlin 1931; Ratcliff 1941; Packard 1942). Following the elk reduction programs of the 1940s, Buttery (1955) concluded that range condition had improved to fair condition, and was stable. After the cessation of elk reductions, Stevens (1980) found stable sagebrush grasslands, but increases in bare ground in grasslands between 1968–1979. Stohlgren et al. (1999) found grazing reduced herbaceous cover slightly, and increased diversity.

A greater level of concern has been recently expressed about elk impacts on riparian willow communities, beaver, and aspen. Aspen stands on the winter range have exhibited little or no regeneration, heavy bark scarring, and mortality (Olmsted 1979, 1997; Stevens 1980; Baker et al. 1997), all attributable to elk browsing. A recent analysis of historical aerial photography showed that over the last 50–59 years willow cover has declined by 19–21% (Peinetti 2000; Peinetti et al., this volume). These decreases were associated with 44–56% decreases in total stream channel density, which was believed to be a consequence of reduced beaver activity. Beaver have declined both on and off the winter range from high levels in 1925–1947 (Warren 1926; Packard 1947b) to current densities which are apparently 90% less than in 1940 (Hickman 1964; Stevens and Christianson 1980; Gense 1997; Zeigenfuss et al., this volume). Some authors have attributed the decline to elk, particularly their negative impacts on willow (Packard 1947b; Gysel 1960; Hess 1993). However, beaver numbers first declined when elk were being controlled below their food-limited carrying capacity.

These concerns led to the inception of several new studies of the elk winter range, including the present study. A 3-year study of elk impacts on upland grasslands and shrublands has shown little impact of herbivory (Zeigenfuss et al., this volume). Few effects have been noted of elk on soil carbon and nitrogen or herbaceous root biomass (Binkley et al., this volume; Schoenecker et al., this volume); however, in willow communities Schoenecker et al. (this volume) found markedly (5x) lower N mineralization outside short-term exclosures located in portions of the winter range judged to have high elk densities. All of the sites were in browsing-suppressed short willow communities. A 5-year study of elk browsing impacts on willow (Peinetti 2000; Singer et al., this volume; Zeigenfuss et al., this volume) has shown large increases in willow growth when protected from elk herbivory. Zeigenfuss et al. (1999) found a continuation of some of the negative vegetation trends observed earlier by Stevens (1980). Olmsted (1997) found further evidence that aspen stands were degrading. Berry et al. (1997) examined whether vegetation on the elk winter range has deviated from pre-Columbian conditions due to elk overabundance. They concluded elk were responsible for aspen and willow declines and decreases in upland range condition, and suggested that the vegetation be protected from herbivory to facilitate recovery from past damage.

The present modeling study was initiated with the specific aims of estimating elk carrying capacity and elk impacts on riparian willow. The more general purpose of this research was to assess the role of elk in the RMNP ecosystem. Ecosystem modeling was used to assess the role of elk in the ecosystem, and the way that ecosystem dynamics have been altered by interactions between elk, climate, and humans. Ecosystem modeling is a comprehensive approach to carrying capacity assessment. It simultaneously addresses different concepts of carrying capacity by explaining ecosystem dynamics in terms of underlying ecosystem processes. The model was used to represent plant and soil responses to herbivory, food limitation of the herbivore population, and predation. It was used to project ecosystem dynamics under past, present, and future management scenarios.

Model Description and Data Inputs

SAVANNA is a spatially explicit, process-oriented model of grassland, shrubland, savanna, and forested ecosystems developed originally for studies in East Africa (Coughenour 1992, 1993). The model has been applied to Elk Island National Park in Alberta (Buckley et al. 1995), the Pryor Mountain Wild Horse Range, Montana (Coughenour 2000), northern Australia (Ludwig et al. 1999), South Africa (Kiker 1998), and Tanzania (Boone et al. 2001). SAVANNA simulates processes at landscape through regional spatial scales over annual to decadal time scales. The model is composed of site water balance, plant biomass production, plant population dynamics, litter decomposition and nitrogen cycling, ungulate herbivory, ungulate spatial distribution, ungulate energy balance, and ungulate population dynamics submodels. Wolf predation and wolf population dynamics submodels are derived from a model used to assess wolf reintroduction into Yellowstone National Park (Boyce and Gaillard 1992; Boyce 1993).

The model was driven by weather data from weather stations in and surrounding the study area. Monthly precipitation and temperature maps were generated from spatial interpolation on elevation corrected data. Historical weather data since 1949 were readily available. Data for 1931–1948 were sparse, however there were key stations with data, including Estes Park, Grand Lake, and Fraser. Data for the period 1910–1930 were reconstructed based upon deviations from normal observed in the data from Fraser, Colorado, which had the most reliable and longest record. Data for the period 1775–1909 were reconstructed from the tree-ring database of Fritts (1991a,b).

SAVANNA requires a vegetation map for the initialization of plant biomass and population variables.

A single-source vegetation map for the entire elk range did not exist, primarily because the elk range extends outside the park boundaries, and includes land from three administrative agencies, the U.S. National Park Service, the U.S. Forest Service (USFS), and the Town of Estes Park. Consequently, a vegetation map was constructed from multiple sources. Vegetation cover maps from RMNP and the Arapahoe-Roosevelt National Forest (ARNF) were combined into a single coverage (Ron Thomas, RMNP GIS lab). Vegetation outside RMNP and ARNF, i.e., on private landholdings, was derived from a vegetation map of Larimer County, Colorado that was developed at Colorado State University from a Landsat-TM scene (McCool 1995; Todd 1995). Disturbed areas, human land uses and areas subsidized by water, were delimited with the aid of satellite data of the normalized difference vegetation index (NDVI). An "undisturbed" vegetation map was created to represent the vegetation cover prior to the settlement of the Estes Valley. Vegetation and land covers of anthropogenic origin on the Larimer County vegetation map were restored to undisturbed conditions. All areas classified as disturbed, urban, golf course, etc., were reclassified as grassland. The Big Thompson river course was markedly altered by development, including the construction of a dam and lake. Historical photographs of the valley before town and dam construction showed the former extent of the river course and riparian floodplain. These features were incorporated into the "undisturbed" vegetation map.

The model was configured to represent ten plant functional groups: upland grasses and forbs, riparian graminoids and forbs, upland shrubs, willow, aspen, ponderosa pine/Douglas fir, lodgepole pine, and subalpine conifers (spruce-fir). The area that was simulated was defined by the combined winter and summer ranges of the elk that winter on the east slope of RMNP, and in the town of Estes Park. Two subherds of elk were simulated, a park subherd and a town subherd, based on information that animals from these subherds exhibit fidelity to these ranges (Lubow et al., this volume). Mule deer were also simulated, primarily to represent their impacts on plants. Their range was assumed to be the elk-defined study area, but with different habitat preferences.

The plant growth model was parameterized from numerous data sources in the literature, and from recent field studies in RMNP. Then it was verified by comparing model outputs to observed biomass data from Hobbs (1979), Fisk et al. (1998), Singer et al. (this volume), and Zeigenfuss et al. (this volume). Comparisons were made for several major vegetation types including: dry grasslands, mesic riparian herbaceous, upland shrubs, willow, low elevation woodlands dominated by ponderosa pine (montane woodland), high elevation woodland and forest dominated by lodgepole pine, Engelmann spruce and subalpine fir, and alpine tundra. Comparisons were made under grazed and ungrazed conditions. The comparisons proved to be generally favorable.

Model Verification: The Control Run for 1949–1998

A simulation was conducted to represent observed ecosystem dynamics for the period 1949–1998. This was referred to as the control run because it represented a set of standard conditions to which results from other model experiments could be compared. Control run output provided additional information for verifying the model's behavior by comparing simulation results to observations. The control run was a calibration run for animal submodels, because key model parameters for diet selection, forage intake, energy use, and population dynamics were calibrated so that model outputs most closely matched observed values.

The simulated elk population was reduced using observed rates of elk offtake by hunter harvest and management removals. The deer population was maintained within a range of 400–600 animals throughout the simulation by removals as necessary.

The snow submodel was verified by comparisons between observed and predicted data at seven SNOTEL stations 1979–1998. The snow model performed satisfactorily at most of the sites.

Water table depths in riparian willow stands (Singer et al. 1999; Zeigenfuss et al., this volume) were used to parameterize model relationships between water table depth and streamflow in the watershed. These relationships were then used in the model to estimate water table depths for different willow sites within each watershed.

The elk population model was calibrated to observed, sightability-corrected count data 1959–1998 (Lubow et al., this volume). The model was calibrated to pass through the higher of the reasonable data points, on the assumption that lower values were undercounts. The model simulated the correct rate of population increase, and most importantly, represented the leveling-off of the park population during 1980–1998 (Fig. 1). This indicates that the model was representing density dependent competition for food, and thus food-limited carrying capacity, correctly. There was a clear decline in the ratio of calves to cows over the period 1949–1998.

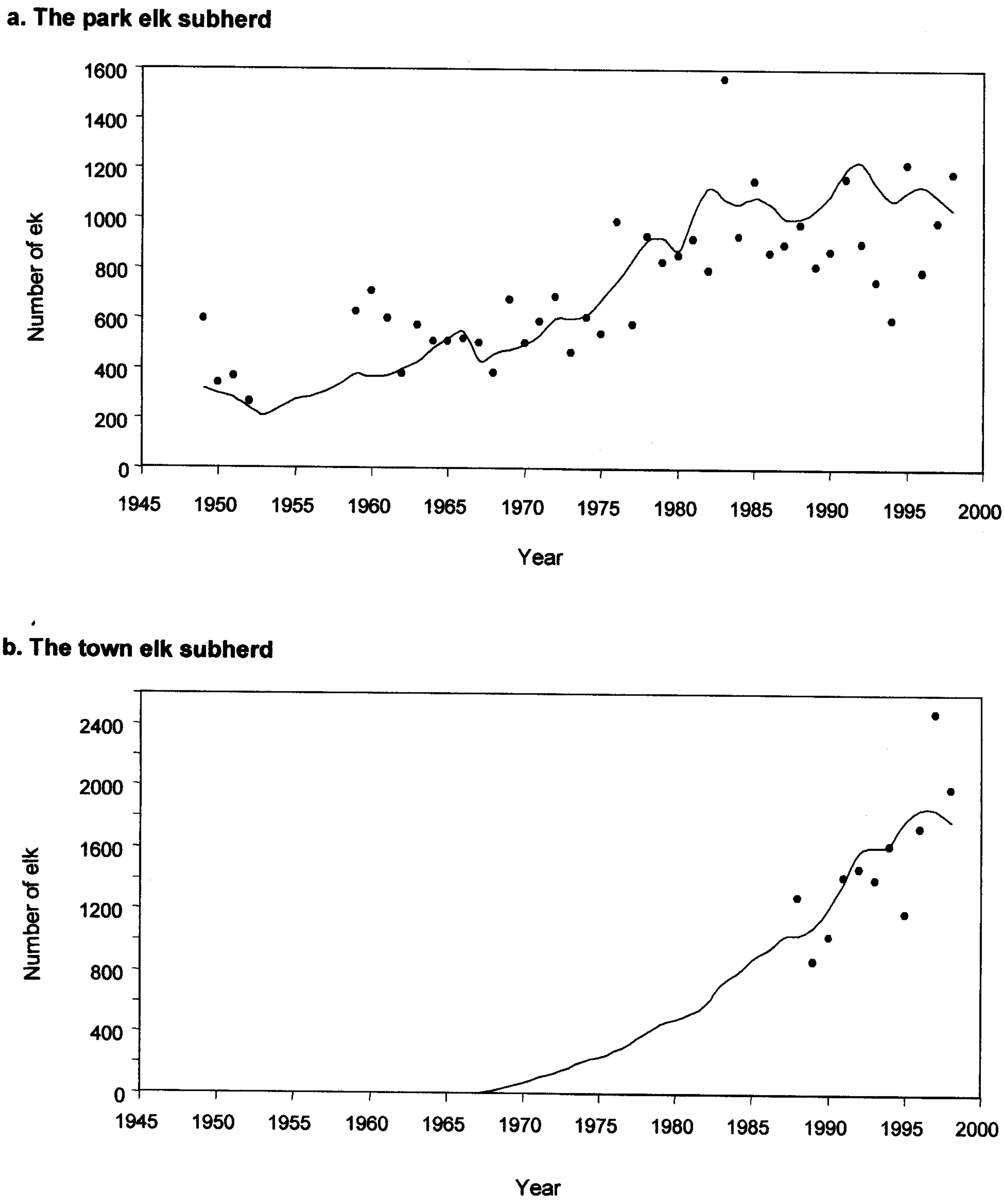


Fig. 1. Simulated (lines) and observed (points) population dynamics for (a) the park elk subherd; and (b) the town elk subherd of the eastern side of Rocky Mountain National Park and the town of Estes Park, Colorado.

This was consistent with data, and with the hypothesis that the elk population was exhibiting a density-dependent limitation on recruitment (Lubow et al., this volume).

Simulated spatial distributions of elk were in agreement with observed data. High densities of up to 90 elk/km^2 were simulated in the Moraine Park area. High densities were also simulated in certain areas of Horseshoe Park, but overall density was less than in Moraine Park. These densities are consistent with the contour maps generated from aerial survey data (Singer et al., this volume), which show density contours of 12–16 elk/km^2 in Horseshoe Park and >90 elk/km^2 in Moraine Park.

Simulated elk diets were consistent with data of Riorden (1948), Hobbs (1979), Stevens (1980), Baker and Hobbs (1982), and Singer et al. (2002).

The model predicted a reasonable spatial distribution of herbaceous biomass over the winter and summer ranges. Peak biomass generally ranged 40–150 g/m^2 on the winter range on grassland, shrubland, and ponderosa pine woodlands. Low production was simulated in the subalpine forests (20–40 g/m^2). Higher biomass levels were simulated on the alpine tundra and subalpine meadows. Aboveground net primary production was not much higher than peak standing crop.

Condition indices of elk reached maximum values each summer. End of winter minima declined over the period in response to increasing density and competition for limited forage. There was considerable variability among winters, reflecting differences in winter severity, and foraging conditions. Condition indices of the town population showed a similar pattern, but when densities were extremely low, winter minima were much higher than observed in the park population. As the town population increased, winter minima decreased markedly.

Model Experiments

Model experiments were conducted for three different time periods: 1775–1910, 1911–1948, and 1949–1998.

The Period Before Reintroduction of Elk (1775–1910)

The period before the reintroduction of elk (1775–1910) included transitions from an ecosystem undisturbed by Euro-American colonists but possibly affected by Native Americans, to an ecosystem that was heavily exploited by early settlers. Beaver trapping occurred prior to 1850, market hunting and extirpation of elk occurred in the 1870s, followed by logging, and heavy livestock grazing throughout the Estes Valley and the elk winter range inside the current park boundaries. Wolves were still present in 1894, but were extirpated well before 1917 (Stevens 1980). Simulation studies of this period were designed to examine the pre-settlement ecosystem, and the impacts of these initial disturbances.

The reconstructed undisturbed vegetation map was used in all of the 1775–1910 runs. Human impacts on ungulates were represented in the model through the imposition of prescribed hunting reductions. To reduce confounding effects, deer were kept at or below 600–700 throughout the entire simulation. Beaver on the elk winter range inside the park were held at 450 throughout. The control run for this period (a run to simulate actual conditions) examined the effects of the extirpation of elk by market hunting. Experimental runs were conducted to examine undisturbed conditions assuming one elk herd, undisturbed conditions assuming two elk subherds limited to the ranges now occupied by park and town subherds, respectively, and the effects of wolves.

When the historic pattern of hunting was imposed, elk were extirpated as specified (Fig. 2a), and in response deer numbers increased and wolves were eliminated due to lack of prey. With no elk hunting, and with wolves (undisturbed conditions), total elk numbers varied between 1,500–3,500 and gradually increased throughout the simulation (Fig. 2b). Distinguishing two subherds indicated the relative sizes of subherds that would be expected in the two ranges. The park subherd varied between 300–800 elk, while the town subherd varied between 1,400–1,500 elk at first, increasing to approximately 1,600–2,000 elk in later years (Fig. 2c). Deer numbers were kept to <200 by wolf predation. Without wolves, total elk numbers increased at first to about 3,800, then numbers exhibited a dynamic equilibrium at approximately 2,800 elk, but with a declining long-term trend due to deteriorating range conditions (Fig. 2d). Elk numbers ended at a similar point with or without wolves, but elk and vegetation conditions were substantially improved in the presence of wolves. Elk condition indices remained higher in winter when wolves were limiting the population compared to when food was limiting the population. Elk mortalities due to starvation were therefore likely to be far less with wolves present.

When elk were hunted to historic levels, dryland herbaceous biomass, i.e., herbaceous layer biomass everywhere on the park elk winter range except in

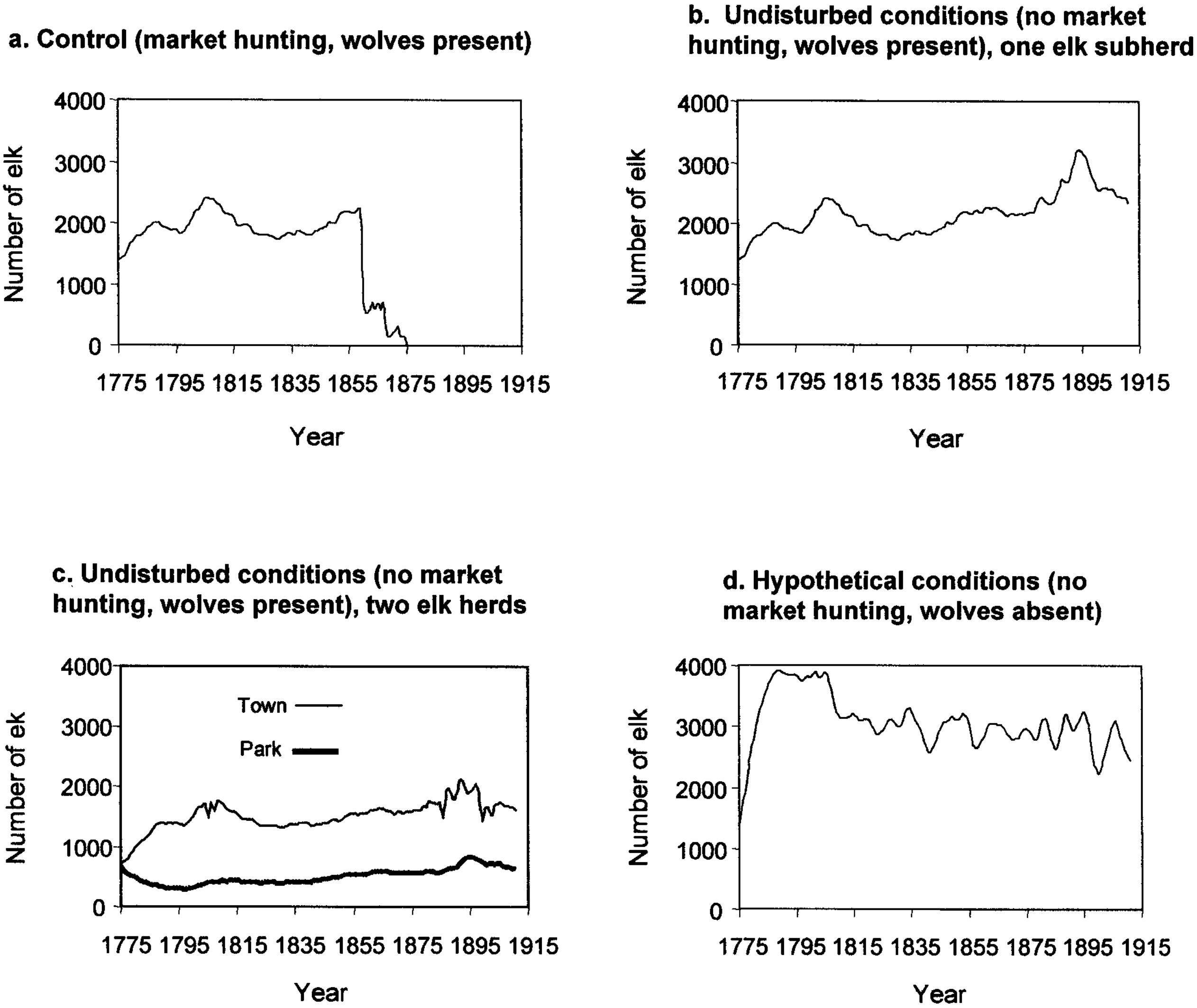


Fig. 2. Elk populations of the eastern elk winter range of Rocky Mountain National Park and the Estes Valley, Colorado, in simulations of the period 1775–1910. All simulations were conducted with undisturbed vegetation and water table conditions and initialized at 1,200 elk (when two subherds were present, 600 in the park and town each).

riparian willow and wet meadows, increased. In undisturbed conditions (no market hunting and wolves present), dryland herbaceous biomass increased and then decreased slightly when elk were limited by wolves. Without wolves, dryland biomass declined gradually throughout the period. With historic elk hunting, willow cover increased to the maximum level (Fig. 3a), while with undisturbed conditions willow cover increased to near-maximal levels (Fig. 3b,c). In contrast, without wolves, willow cover declined (Fig. 3d). Aspen increased markedly following the extirpation of elk (Fig. 3a). With undisturbed conditions, aspen cover decreased even when wolves were present (Fig. 3b,c). The aspen decline was not accelerated by lack of wolves (Fig. 3d). This suggests that aspen cover at the inception of the park and elk reintroduction, could have been higher than if there were no elk extirpations.

To summarize the assessment of 1775–1910, it is very plausible for wolves and other predators to have maintained elk numbers below food-limited carrying capacity, but still at moderately high numbers, maintained by increased productivity of the vegetation compared to current conditions. Increased cover of willow could be supported, but beaver activities would be critical to maintenance of high water tables. Aspen would have had a difficult time becoming established or surviving the predator-limited densities of elk and mule deer on the core, lower elevation portions of the winter range. Purported evidence for aspen in those locations prior to 1870 should be carefully examined. Elk extirpation could have been a primary cause for the emergence of aspen stands in those locations. Effects of elk on beaver populations, or of bison impacts on elk winter forage were not considered.

Establishment of the Park and Reintroduction of Elk (1911–1948)

The period 1911–1948 included the inception of the park, the reintroduction of elk, and early conservation efforts. For most of the period, elk hunting was absent, or minimal. Hunting offtake was insignificant until 1941, and was 90–122 elk per year during the period 1941–1945 (Stevens 1980). The first significant management reduction did not occur until 1945, when 301 elk were removed (Stevens 1980). There were no reductions between 1946–1948, and hunting offtake was reduced to 20–80 per year. Thus, this was mainly a period of elk protection, with the first efforts of elk management occurring at the end of the period. Much of the elk winter range within the current park boundary was affected by human settlement, livestock grazing, haying, and resorts. Willow habitats were drained, and willow was removed to create pastures or hayfields. I assumed that between 1911–1931, the elk herd was mainly restricted to the area east of the current park boundary due to lack of access to the core grasslands in Moraine Park and Horseshoe Park, as these were grazed by domestic stock or hayed. Elk were introduced into the model in 1913 and 1914. Deer were kept at the 600–700 level until the period 1927–1942, when the population increased to 1,000–1,200 animals (Stevens 1980).

In the control run for this period, elk increased to about 800 animals by 1934, and then kept within a similar range to the estimated values. The undisturbed simulation began with the elk numbers simulated at the end of the undisturbed 1775–1910 run, and with wolves present. In this run, elk also had access to the full winter range, as opposed to being precluded from the core winter range inside the park. Wolves held the park subherd to 500–1,000 elk, while the town subherd increased to 2,500 and then declined to 1,200. Without wolves, the park subherd increased to 1,500, and the town subherd increased to about 2,700 before declining markedly to approximately 1,500.

There were few differences among dryland herbaceous biomass amounts in the different scenarios during this period. Willow cover increased to high levels in all runs where elk started out at zero, even with no elk reductions. The initial period when elk were absent or present at low numbers was sufficient for willow to reach tall stature. Once willow reached tall stature, it for the most part escaped herbivory. Subsequent conversion to short willow depended on the gradual mortality of old plants, and suppression of replacement plants. With the observed number of elk, and high water tables, the model did not simulate a decrease in willow during 1911–1948. In particular, the model could not explain willow declines under the number of elk present up until 1930. If water tables were high, the model only simulated willow declines during 1911–1930 if elk were assumed to be in the 500–1,000 range for the entire period, which was unrealistic. Willow declines were simulated during this period only when hydrology was altered. Humans likely played a significant role in these alterations.

In the control run, aspen increased at first but in about 1925–1930 began to decrease. In hypothetical runs with no elk or beaver present, the decrease did not occur. The results suggested that the combination of elk and beaver was responsible for the decline. In the undisturbed

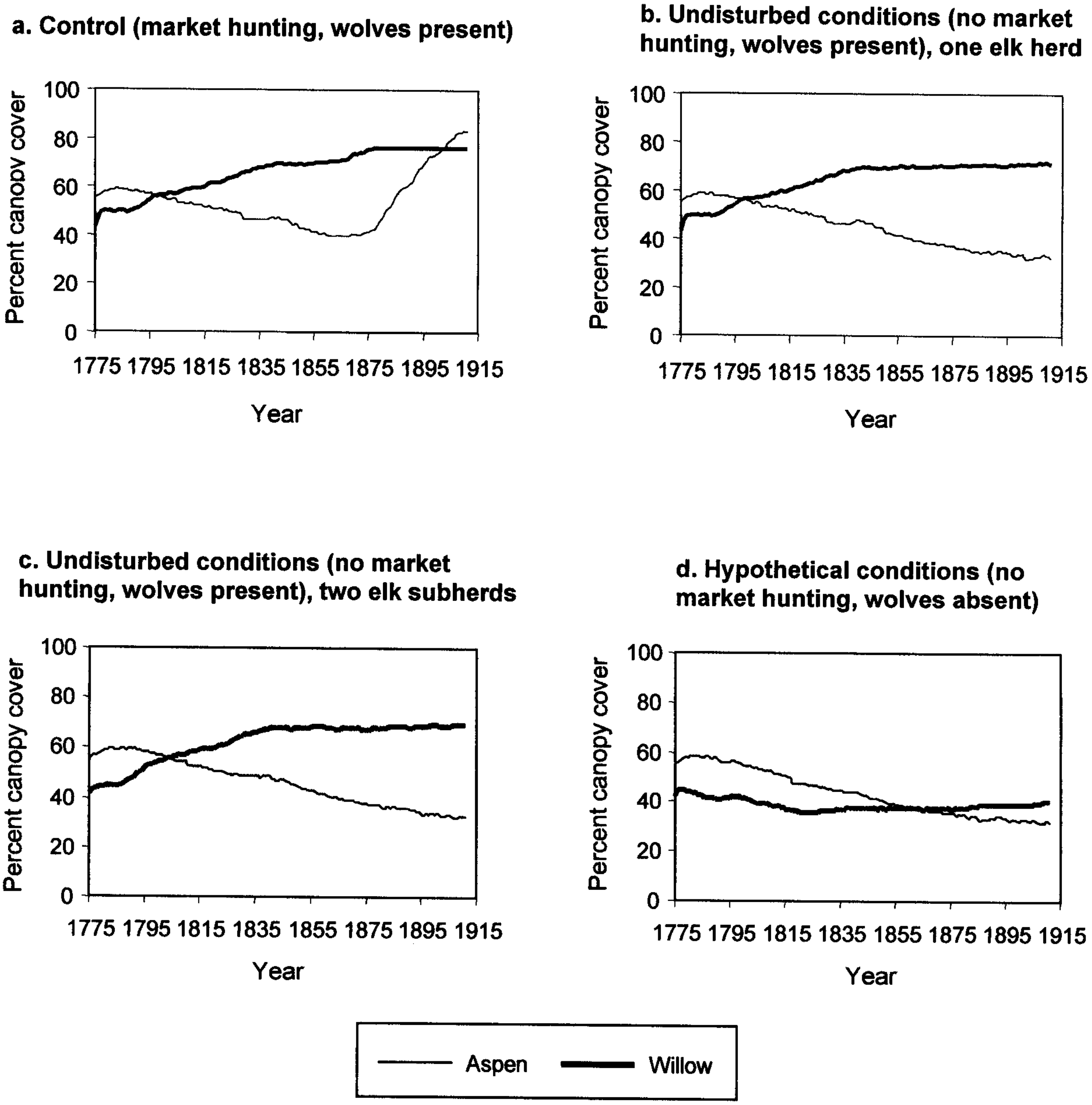


Fig. 3. Willow and aspen cover of the elk winter range of Rocky Mountain National Park and Estes Valley, Colorado, in simulations of the period 1775–1910. Cover reported as mean canopy cover within the grid-cells having those vegetation types. All simulations were conducted with undisturbed vegetation and water table conditions.

run with wolves, aspen remained steady at the low initial value, suggesting that aspen would be present at lower abundances in some locations on the core winter range.

The assessment of 1911–1948 revealed the importance of human disturbances both before and after 1911, in moving the system into what could be considered to be an alternate stable state. Livestock grazing, draining of wetlands, removal of elk and wolves, and compression of elevated numbers of beaver into reduced willow cover, all combined to reduce willow cover in Moraine and Horseshoe Parks further. Aspen declined as well, due to the combined effects of elk and beaver, but the initial presence of some of the aspen that declined in this period could have been a product of earlier elk extirpation.

Effects of Elk, Elk Management, and Simulated Wolf Predation (1948–1998)

Simulation experiments for 1949–1998 were intended to investigate the effects of elk, elk management, and wolves. In these runs, two elk populations and ranges were simulated, the park and the town populations. The first experiment was to allow elk populations to grow unchecked. The park population grew to a food-limited carrying capacity earlier than in the control run, and food-limited population sizes were slightly higher in the 1960s and 1970s than in the 1980s and 1990s. Food-limited carrying capacity of the park subherd appeared to be in the range of 1,000–1,300 elk. The town population increased to a slightly higher level than in the control run (1,900 vs. 1,800) before declining. In the undisturbed run with wolves, the park elk population was held to 300–500. The town population increased from 1,000 to 1,800, but then predation decreased the population to about 1,200. Wolf numbers varied between 14–17 throughout. Elk body condition in the run with no elk reductions was lower in winter than in the control run, throughout the simulation. In the undisturbed run, body condition was maintained at a higher level, with the exception of several severe winters.

When elk and deer were not reduced, there was about 10% less grass and 30% less forb biomass on drylands than in the control run by the end of the period. These results are consistent with Buttery's (1955) observations of modest increases in range conditions in some areas due to elk removals. In the undisturbed run, there was about 8% more grass and 5% more forb biomass than in the control run. Willow cover decreased with no elk reductions, while it remained constant in the control. In the undisturbed run, willow cover increased. All willow locations in the undisturbed run attained cover >60%. Reducing water tables had a negative effect on willow cover at three of the locations, but cover at those locations declined to lower values with elk than without elk. In additional experiments conducted to further examine the effects of water table levels, using undisturbed water tables led to an increase in willow compared to the control run which used current water table conditions. Conversely, switching to current water table conditions in the otherwise undisturbed run led to markedly lower willow covers. In the control simulation, aspen cover declined about 15%. With no elk reductions, the decline occurred earlier. In the undisturbed run with wolves, aspen cover also declined due to elk herbivory. In a hypothetical simulation with no elk present, aspen increased.

It seems likely, therefore, that the elk reductions in the 1940s–1950s brought about modest range improvement, and protected some, but not all willows and aspen. The reductions did not appear to have led to a restoration of willow to its former range, primarily because elk reductions do not address the problem of lowered water tables. While the elk reductions would have created opportunities for aspen recruitment in some areas, it seems unlikely that they would have promoted aspen regeneration on the primary elk concentration areas. While there is some evidence that elk reductions promoted aspen regeneration (Olmsted 1979; Baker et al. 1997), the spatial locations of such regeneration are critical to this interpretation. For example Stevens (1980) suggested that regeneration occurred in places where elk were shot and thus avoided using, and Olmsted (1979) showed that aspen only regenerated in areas with <50% utilization by elk.

Experiments with Elk and Beaver Densities

A factorially designed experiment was conducted in which elk and beaver densities were varied in all possible combinations, to assess their relative effects on plants. A response surface of willow cover generated from the results showed that elk and beaver can both have negative effects, but beaver effects are negligible at low elk densities. Increasing beaver had little impact on willow below 400 elk. In the range of predator-limited elk carrying capacity (400–800 elk), less than 450 beaver had little impact on willow.

Alternative Elk Management and Vegetation Fencing Scenarios

Alternative elk management and vegetation fencing scenarios were simulated by running the model for 50 years, starting in 1994, using weather randomly selected from data for the period 1949–1998. All runs began with current conditions, including current herbivore numbers, willow sizes and densities, and soil water table depths. There were three elk reduction scenarios. The park elk subherd was either never reduced, reduced to 600–800, or reduced to 200–400. In all elk reduction scenarios, the town population was reduced to 1,000–1,200. Beaver were assumed to start at current levels, and then gradually be restored to historic levels (450) over a 25-year period. Aspen and willow within the park boundary were either unfenced, or fenced to exclude elk and deer, but not beaver herbivory.

With no reductions of the park or town elk subherds, the park elk population fluctuated between 800–1,100 animals, consistent with the range previously estimated to be the food-limited carrying capacity (Fig. 4a). The town population increased at first to 2,400, then varied between 1,400–2,000. Fencing all of the willow and aspen inside the park reduced the food-limited carrying capacity of the park population by approximately 30–40% (Fig. 4b). Elk body condition in the winter was low when elk were not reduced. Reducing elk to 600–800 raised winter body conditions moderately, while reductions to 200–400 raised body conditions markedly.

Dryland herbaceous biomass remained essentially constant when elk were not reduced. However, when elk were reduced to 600–800, biomass increased slowly, over the entire period. Reducing elk to 200–400 caused a faster rate of biomass increase, and biomass was still increasing after 50 years. Fencing had no discernable effects on dryland herbaceous biomass. Without fencing, aspen declined to similar levels irrespective of elk reductions (Fig. 5a,c,e). During the years when aspen were protected by fencing, cover increased markedly (Fig. 5b,d,f). However, when the fence was removed, aspen began to decline once again, in all elk reduction treatments. Willow continued to decline when elk were not reduced (Fig. 5a), increased slightly when elk were reduced to 600–800 (Fig. 5c), and markedly increased when elk were reduced to 200–400 (Fig. 5e). Fencing resulted in a large increase in willow cover irrespective of reductions (Fig. 5b,d,f). After the fence was removed, willow began to decline when elk were not reduced and when reduced to 600–800 (Fig. 5d). In contrast, when elk were reduced to 200–400, willow cover remained at a high level after the fence was removed (Fig. 5f).

Increasing water table heights had little positive benefit when elk were not reduced and willow were unprotected by fencing (Fig. 6a). With fencing, the added water supported higher willow cover during the fenced period, which was sustained after the fences were removed, even with no elk reductions (Fig. 6b). With no fencing, higher water tables led to small increases in willow cover when elk were reduced to 600–800, and larger increases in willow cover when elk were reduced to 200–400 (Fig. 6c,e). With fencing, high water tables led to further increases in willow cover when fences were removed, and elk were reduced (Fig. 6d,f). Increased water table depth had no effect on aspen, because it was assumed that elevated water tables only occurred in riparian willow and wet meadow habitats, and not in aspen habitats.

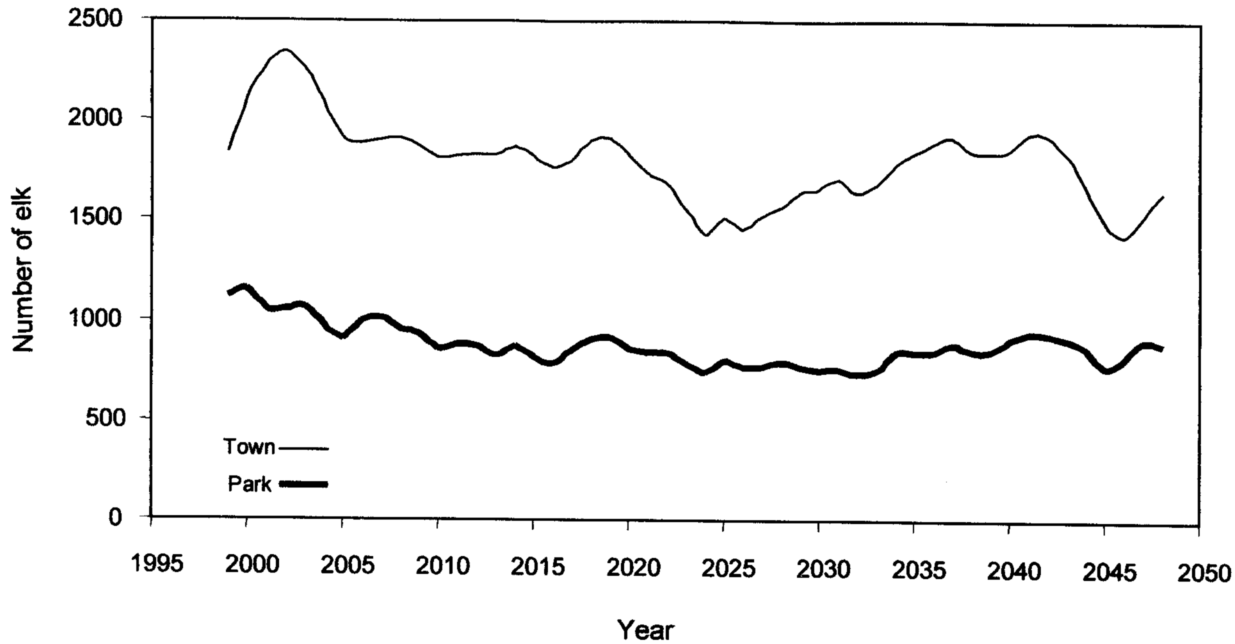
Beginning with current vegetation, soil water table depths, and elk numbers, a hypothesized wolf reintroduction quickly reduced elk numbers in both the town and park subherds. After 15 years, the system stabilized at 14 wolves, about 200 elk in the park population, and about 1,000 elk in the town population. Wolves held elk to lower levels in future vs. historic runs because of deteriorated range conditions. Deer were held to 200.

The assessment of alternative management scenarios showed that a marked elk reduction to levels which may be lower than those present in pre-settlement times, or fencing, would achieve a recovery of willow, but only in locations where water tables are still elevated. Reintroduction of beaver or other manipulations to raise water tables would be required to achieve a complete recovery. Aspen cover could be increased by fencing or severe elk reductions, however, elk numbers would have to be maintained very low, or once fences are taken down, aspen cover on the core winter range would again decline.

Sensitivity to Wolf Submodel Parameters

Simulations were performed to examine sensitivity to the wolf submodel parameters. The model was particularly sensitive to the parameter that represents how wolves control their own density through territoriality, the fraction of prey mortality that is compensatory vs. additive, and the way predation is distributed among age/sex classes. It was possible to find plausible parameter values that resulted in diminished or no effects of predation on elk population size, as well as values that resulted in lower elk numbers than noted above.

a. No elk reductions; no fences



b. No elk reductions; fence all willow and aspen inside the park for first 25 years

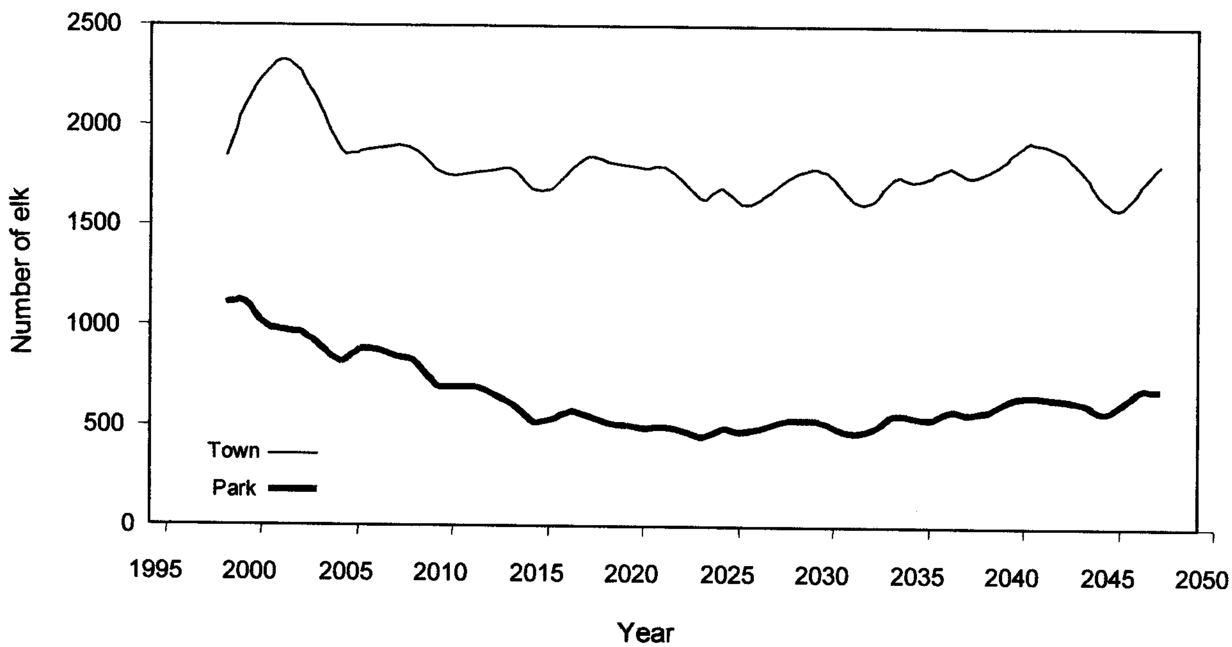


Fig. 4. Elk population dynamics under different future management scenarios for the elk winter range population of Rocky Mountain National Park and the Estes Valley, Colorado. Beaver population dynamics are prescribed, and are gradually restored to natural levels by 2030. (a) No elk reductions, no fencing; and (b) no elk reductions, fence all willow and aspen inside the park for the first 25 years. Elk reduction scenarios are not shown because elk populations in the park were held at either 600–800 or 200–400 animals (depending on the scenario) and the town population was held between 1,000–1,200.

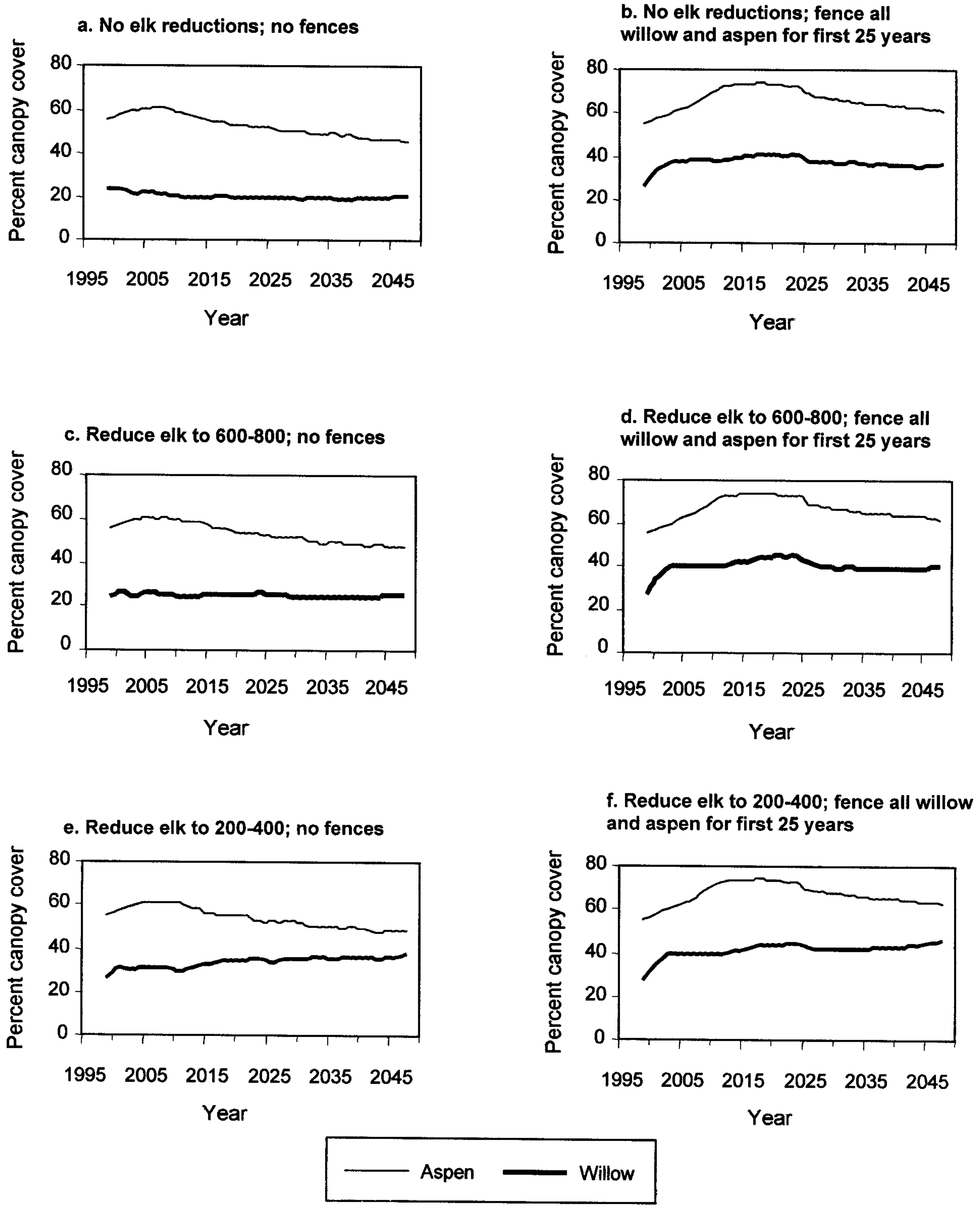


Fig. 5. Responses of willow and aspen to management scenarios for the elk winter range population of Rocky Mountain National Park and the Estes Valley, Colorado, using randomly selected weather from 1949–1998 and current water tables, for 50 years expressed as mean canopy cover within grid-cells of that vegetation type. See Fig. 6 for the same model scenarios with increased water tables.

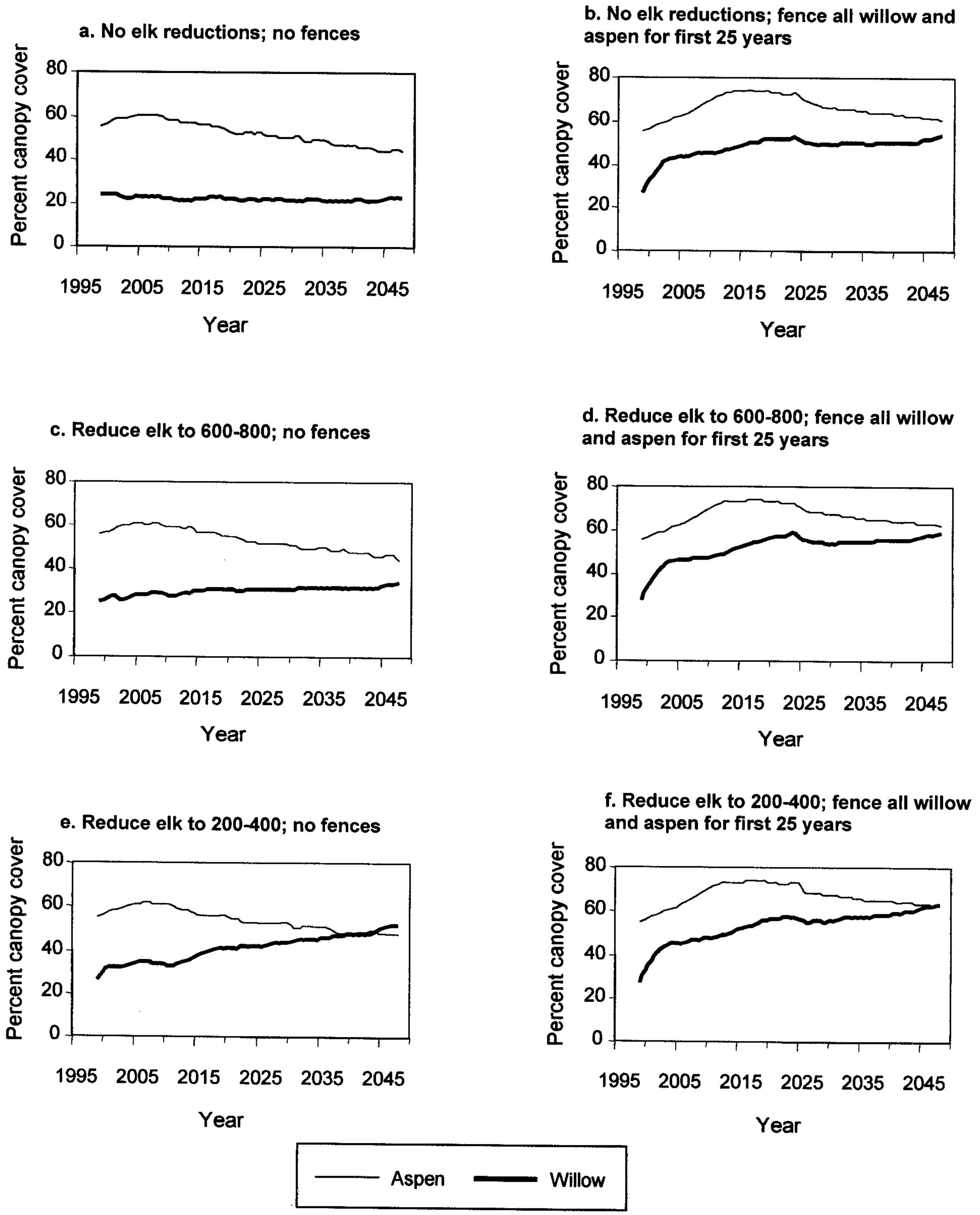


Fig. 6. Responses of willow and aspen to management scenarios for the elk winter range population of Rocky Mountain National Park and the Estes Valley, Colorado, using randomly selected weather from 1949–1998 and increased water tables, for 50 years expressed as mean canopy cover within grid-cells of that vegetation type. See Fig. 5 for the same model scenarios with current water tables.

The model showed that the situation in RMNP is more complex than the simple plant-herbivore equilibrium predicted by natural regulation theory. While the elk-grassland subsystem may reach an equilibrium, that equilibrium would probably not have developed in the presence of wolves and other predators. Instead, a different dynamic equilibrium would be expected, involving interactions among three trophic levels. It would not be totally accurate to refer to this as a predator-limited number of elk, because the productivity of the forage base also has an influence. In a more productive system, there would be more herbivores and more predators alike, up until a limit on predator and possible herbivore numbers imposed by other factors aside from food, such as behavioral spacing. Because the tri-trophic equilibrium involves fewer elk than the bi-trophic equilibrium, there could be ramifications for plant species that are not necessarily limiting the elk population in a bi-trophic system, in particular aspen and willow.

Management Implications

Management of ungulates in U.S. National Parks is directed by the enabling legislation of the U.S. Congress (the Organic Act of 1916) which states that National Parks are "to conserve the scenery and the natural and historic objects and the wildlife therein and to provide for the enjoyment of the same in such a manner and by such means as will leave them unimpaired for future generations." In this view, managers must conserve the vegetation structure that was a product of pre-settlement climate, soils, and ungulate herbivory. In Yellowstone and RMNP, this vegetation structure is thought to be characterized by greater abundances of aspen and willow than are present at the food-limited carrying capacities of their elk populations. Another view places more emphasis on the conservation of natural processes, and recognizes that ecosystems are dynamic, not static entities (Houston 1982; McNaughton 1996; Boyce 1998; Sinclair 1998; Huff and Varley 1999). National Park Service Management Policies (NPS 2001) state that the Service will try to maintain all the components and processes of naturally evolving park ecosystems, and will rely on natural processes to maintain native species and natural fluctuations in populations whenever possible. Natural processes are those which characterize ecosystems in general, rather than a specific ecosystem at a certain point in time. Thus, there is a fundamental policy discord, between a strict reading of the NPS Organic Act, and what many believe is a more modern and scientifically informed view about ecosystem dynamics in nature.

Ultimately the choice of elk management tactics reduces to a decision between trying to reconstruct, and then maintain, the vegetation structure which is believed to have been characteristic of the pre-settlement ecosystem, or allowing ecosystem processes to unfold with a minimal amount of human intervention so long as indigenous species are conserved. The question of which would be more natural or desirable cannot be answered here. The model provided insight into how a pre-settlement ecosystem might have looked and functioned, but it did not consider whether or not such an ecosystem is natural in the present time, most appropriate to NPS policies, or desirable to the American people who are the true owners of RMNP.

Literature Cited

Baker, D. L., and N. T. Hobbs. 1982. Composition and quality of elk summer diets in Colorado. Journal of Wildlife Management 46:694–703.

Baker, W. L., J. A. Munroe, and A. E. Hessl. 1997. The effects of elk on aspen in the winter range in Rocky Mountain National Park. Ecography 290:155–165.

Benedict, J. B. 1992. Footprints in the snow: High-altitude cultural ecology of the Colorado Front Range, USA. Arctic and Alpine Research 24:1–16.

Benedict, J. B. 1999. Effects of changing climate on game-animal and human use of the Colorado high country (USA) since 1000 BC. Arctic, Antarctic, and Alpine Research 31:1–15.

Berry, J., D. Decker, J. Gordon, R. Heitschmidt, D. Huff, D. Knight, W. Romme, and D. Swift. 1997. Science-based assessment of vegetation management goals for elk winter range. Environment and Natural Resources Policy Institute, Colorado State University, Ft. Collins.

Boone, R., M. B. Coughenour, K. A. Galvin, and J. E. Ellis. 2001. Addressing management questions for Ngorongoro Conservation Area, Tanzania, using the Savanna modeling system. African Journal of Ecology. In press.

Boyce, M. S. 1993. Predicting the consequences of wolf recovery in Yellowstone National Park. Pages 234–269 *in* R. S. Cook, editor. National Park Service Science Monograph No. 22.

Boyce, M. S. 1998. Ecological-process management and ungulates: Yellowstone's conservation paradigm. Wildlife Society Bulletin 26:391–398.

Boyce, M. S., and J. M. Gaillard. 1992. Wolves in Yellowstone, Jackson Hole, and the North Fork of the Shoshone River: Simulating ungulate consequences of wolf recovery. Pages 4.75–4.115 *in* J. Varley and W. G. Brewster, editors. Wolves for Yellowstone? A report to the U.S. Congress. Vol. IV, Research and Analysis. National Park Service, Yellowstone National Park.

Buckley, D. J., F. Schreiner, M. Coughenour, and C. Blyth. 1995. The ecosystem management model: Integrating ecosystem simulation modeling and Arc/Info in Parks Canada. *In* GIS and environmental modeling: Progress and research issues. Proceedings of the Second International Conference on Integrating GIS and Ecological Modeling, Breckenridge, Colo.

Buttery, R. F. 1955. Range conditions and trends resulting from winter concentrating of elk in Rocky Mountain National Park. M.S. Thesis. Colorado State University, Ft. Collins.

Coughenour, M. B. 1992. Spatial modeling and landscape characterization of an African pastoral ecosystem: A prototype model and its potential use for monitoring drought. Pages 787–810 *in* D. H. McKenzie, D. E. Hyatt, and V. McDonald, editors. Ecological Indicators, Volume 1. Elsevier Applied Science, London and New York.

Coughenour, M. B. 1993. The SAVANNA landscape model – documentation and user's guide. Natural Resource Ecology Laboratory, Colorado State University, Ft. Collins.

Coughenour, M. B. 2000. Ecosystem modeling of the Pryor Mountain Wild Horse Range. Report to USGS, Biological Resources Division, National Park Service, and Bureau of Land Management. Natural Resource Ecology Laboratory, Colorado State University, Fort Collins. 55 pp + 100 figs.

Dixon, J. S. 1939. The elk problem at Rocky Mountain National Park. Typewritten. Files at Rocky Mountain National Park.

Estes, M. 1939. The memoirs of Estes Park. Colorado State College Library, Library Bulletin No. 6. Fort Collins, Colo. (Reprinted in: Colorado Magazine 16[4]:121–132).

Fisk, M. C., S. K. Schmidt, and T. R. Seastedt. 1998. Topographic patterns of above- and belowground production and nitrogen cycling in alpine tundra. Ecology 79:2253–2266.

Fritts, H. C. 199la. Reconstructing large-scale climatic patterns from tree-ring data: A diagnostic analysis. University of Arizona Press, Tucson.

Fritts, H. C. 1991b. Large scale climate reconstructions from tree-rings. International Tree-Ring Data Bank. IGBP PAGES/World Data Center-A for Paleoclimatology Data Contributions Series #91-011. NOAA/NGDC Paleoclimatology Program. Boulder, Colo.

Fryxell, F. M. 1928. The former range of the bison in the Rocky Mountains. Journal of Mammalogy 9:129–139.

Gense, J. 1997. Unpublished data. Files, Rocky Mountain National Park.

Guse, N. G., Jr. 1966. Administrative history of an elk herd. M.S. thesis. Colorado State University, Ft. Collins.

Gysel, L. W. 1960. An ecological study of the winter range of elk and mule deer in the Rocky Mountain National Park. Journal of Forestry 58:696–703.

Hess, K. Jr. 1993. Rocky times in Rocky Mountain National Park. University Press of Colorado, Niwot.

Hickman, S. D. 1964. A beaver census of Moraine Park, Rocky Mountain National Park. Unpublished, Colorado State University. 15 pp.

Hobbs, N. T. 1979. Winter diet quality and nutritional status of elk in the upper montane zone, Colorado. PhD. dissertation, Colorado State University, Ft. Collins.

Houston, D. B. 1982. The northern Yellowstone elk: Ecology and management. MacMillan Press.

Huff, D. E., and J. D. Varley. 1999. Natural regulation in Yellowstone National Park's northern range. Ecological Applications 9:17–29.

Keigley, R. B., and F. H. Wagner. 1998. What is natural? Yellowstone elk population, a case study. Integrated Biology 1:133–148.

Kiker, G. A. 1998. Development and comparison of Savanna ecosystem models to explore the concept of carrying capacity. PhD. thesis, Cornell University, Ithaca, New York.

Loring, J. A. 1893. Field notes on a trip to Estes Park, May 28 to June 3, 1893. U.S. Biological Survey.

Ludwig, J. A., M. B. Coughenour, A. C. Liedloff, and R. Dyer. 1999. Modeling the resilience of Australian savanna systems to grazing impacts. Pages 771–776 *in* L. Oxley, F. Scrimgeour, and A. Jakeman, editors. MODSIM 99, International Congress on Modeling and Simulation Proceedings. Vol. 3. Modeling Society of Australia and New Zealand, Inc.

McCool, M. J. 1995. Classification of the Cache La Poudre watershed using Landsat thematic mapper data and ancillary spatial data. M.S. thesis. Colorado State University, Ft. Collins.

McLaughlin, J. S. 1931. First annual spring wildlife report. Typewritten files. Rocky Mountain National Park.

McNaughton, S. J. 1996. Book review – Wildlife policies in the U.S. National Parks. Journal of Wildlife Management 60:685–687.

Mills, E. A. 1924. The Rocky Mountain National Park: A history. Colorado Associated University Press, Boulder.

National Park Service. 2001. Management policies. U.S. Government Printing Office. Washington, D.C.

Olmsted, C. E. 1977. The effect of large herbivores on aspen in Rocky Mountain National Park. M.S. thesis. University of Colorado, Boulder.

Olmsted, C. E. 1979. The ecology of aspen with reference to utilization by large herbivores in Rocky Mountain National Park. Pages 89–97 *in* M. S. Boyce and L. Hayden-Wing, editors. North American elk. University of Wyoming Press.

Olmsted, C. E. 1997. Twenty years of change in Rocky Mountain National Park elk winter range aspen. Report to U.S. National Park Service, Rocky Mountain National Park.

Packard, F. M. 1942. Wildlife and aspen in Rocky Mountain National Park, Colorado. Ecology 23:478–482.

Packard, F. M. 1947a. A study of the deer and elk herds of Rocky Mountain National Park, Colorado. Journal of Mammalogy 28:4–12.

Packard, F. M. 1947b. A survey of the beaver population of Rocky Mountain National Park, Colorado. Journal of Mammalogy 28:219–227.

Peinetti, H. R. 2000. Riparian willow dynamics and their interaction with environmental and biological factors in the elk winter range of Rocky Mountain National Park (Colorado) – a multiscale analysis. PhD. dissertation. Colorado State University, Ft. Collins.

Ratcliff, H. M. 1941. Winter range conditions in Rocky Mountain National Park. Transactions of the North American Wildlife and Natural Resources Conference 6:132–139.

Riordan, L. E. 1948. Deer-elk survey. Colorado Game and Fish, Federal Aid Quarterly Report, pp 14–30.

Sage, R. 1846. Scenes in the Rocky Mountains, and in Oregon, California, New Mexico, Texas, and the grand prairies; or, Notes by the way, during an excursion of three years, with a description of the countries passed through, including their geography, geology, resources, present condition, and the different nations inhabiting them. By a New Englander. Carey & Hart, Philadelphia.

Sinclair, A. R. E. 1998. Natural regulation of ecosystems in protected areas as ecological baselines. Wildlife Society Bulletin 26:399–409.

Singer, F. J., T. Elliot, M. Coughenour, J. Welker, D. Binkley, D. Valentine, S. Williams, L. Zeigenfuss, K. Alstad, M. Kaye, R. Menezes, R. Peinetti, and R. Rochelle. 1999. Large mammalian herbivores, plant interactions, and ecosystem processes in Rocky Mountain National Park. Fourth Annual Report. U.S. Geological Service, Biological Resources Division, Ft. Collins, Colo.

Singer, F. J., G. Wang, and N. T. Hobbs. 2002. The role of grazing ungulates and large, keystone predators on plants, community structure, and ecosystem processes. *In* R. G. Anthony and C. Zabel, editors. Large mammal communities in U.S. western coniferous forests. Cambridge University Press.

Sprague, A. E. 1925. Game more plentiful now than 50 years ago in Estes Park region. Estes Park Trail. June 5, 1925.

Stevens, D. R. 1980. The deer and elk of Rocky Mountain National Park: A 10-year study. ROMO-13. Report to National Park Service, Rocky Mountain National Park.

Stevens, D. R., and S. Christianson. 1980. Beaver populations on east slope of Rocky Mountain National Park. Special report. U.S. National Park Service. Rocky Mountain National Park.

Stohlgren, T. J., L. D. Schell, and B. Vanden Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecological Applications 9:45–64.

Todd, S. W. 1995. Classification of the Laramie and Big Thompson watersheds using Landsat 5 TM imagery and ancillary GIS digital data. Colorado Division of Wildlife.

Wagner, F., R. Foresta, R. B. Gill, D. R. McCullough, M. R. Pelton, W. F. Porter, and H. Salwasser. 1995. Wildlife policies in the U.S. national parks. Island Press, Washington, D.C.

Warren, G. A. 1926. Notes on the beaver in Estes Park, Colorado. Roosevelt Wildlife Annals 1:193–234.

Zeigenfuss, L. C., F. J. Singer, and D. Bowden. 1999. Vegetation responses to natural regulation of elk in Rocky Mountain National Park. Biological Science Report USGS/BRD/BSR1999-0003. U.S. Government Printing Office, Denver, Colo.